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Can dung beetles from the palaeoecological and archaeological record indicate herd concentration and the identity of herbivores?

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ABSTRACT

We present the results from two analogue studies that examine two aspects of dung beetle populations. Firstly, the degree to which the proportions of dung beetles in terrestrial faunas may reflect herd concentration is assessed by comparing modern sub-fossil faunas retrieved from a range of small ponds at Dunham Massey, Cheshire and Epping Forest in London. These studies suggest that it may be possible to use the proportions of 'dung beetles' recovered to differentiate high from low density grazing pressures in the palaeoentomological and archaeoentomological record.

A second study examines the insect faunas recovered from modern samples of dung from a range of bovids, cervids, suids and equids, chosen to replicate, as closely as possible, Pleistocene taxa. These include the famous Chillingham cattle herd from Northumberland and herds of red deer, wild boar and Konik horses from Kent. When the numbers of individuals and the nature and range of beetles in the whole fauna are considered, it may be possible to differentiate between the dung of a range of different animals. A number of limitations with the present study, their implications and the future potential of this type of study are outlined.

1. Introduction

'Dung beetles', taken here to indicate a broad group of different genera whose members are associated with dung (see below), are routinely recovered, sometimes in large numbers, from a range of palaeoecological and archaeological Pleistocene and Holocene deposits. Typically, their presence is only interpreted as providing an indication that grazing and pasture areas were present in the landscape. However, this is a restricted use of a set of insects that have greater interpretative potential (see Robinson, 1983). In this paper, we attempt to establish whether it is possible to broaden the role that 'dung beetles' play in archaeological and palaeoecological interpretations. Dung beetles, *sensu stricto,* are members of the Scarabaeidae family (representing the genera *Geotrupes*, *Onthophagus* and *Aphodius*) which feed, develop, and live in the dung of herbivores (Jessop, 1986). Animal dung is also utilised as a habitat by a diversity of other beetles such as the Histeridae 'hister beetles', a range of Hydrophilidae (for example *Sphaeridium scarabaeoides* and various *Cercyon* species) and Staphylinidae 'rove beetles'. We include this expanded list of taxa under the heading 'dung beetles' throughout this paper to reflect this wider dung-related community.

This paper will also present the results from two modern analogue studies, compare these with results from a previous study and discuss how 'dung beetles' appear to have had a more significant role to play in the interpretation of sub-fossil insects from a range of Pleistocene, Holocene and archaeological sites than previously suggested.

2. Rationale

2.1. Showing the potential: research issues

The potential of 'dung beetle' studies is brought into focus by three current archaeological and palaeoecological research issues.

The late Russell Coope identified a large number of 'dung beetles' from numerous Pleistocene sites – especially interglacial sites

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- dating from *circa* one million years ago up to 12,000 years ago. Coope's main emphasis was the use of Coleoptera recovered from these deposits to indicate the nature of climatic conditions and long-term climate change (e.g. Coope, 1961, 1977, 2001, 2010; Atkinson et al. 1987; Elias, 2010). 'Dung beetles' were often used to indicate the presence of herds of grazing animals in the vicinity of the sample site, but the ecology of the species recovered was only investigated when they had specific biogeographical importance. The best example of this is *Aphodius holdereri* (Reitter), which is commonly encountered in cold- climate Pleistocene deposits but which is today limited to a few valleys in Tibet and North-western China (Coope, 1973). However, little emphasis has been placed on the past biogeography and diachronic changes in the abundance of these 'dung beetles' and other species between the various interglacials, interstadials, and stadials throughout the Pleistocene. The detailed ecology of the 'dung beetles' recovered has also remained largely unexplored. Given the recent research interest in the role of herbivores in structuring Pleistocene and Holocene landscapes and their effects on ecosystems, (e.g. Vera, 2000; Gill et al. 2009; Johnson, 2009; Rule et al. 2012; Jeffers et al. 2012), this is potentially an area of significant research interest and one in which fossil beetles can make a meaningful contribution.

In a recent reappraisal of Coope's results from a range of English interglacial sites (Whitehouse et al. 2013, and unpublished data) it is surprising to note that, particularly during the Last (Ipswichian) Interglacial (correlated with Marine Isotope Stage [MIS] 5e 128,000–116,000 years), many of the abundant dung beetle species (for example *Caccobius schreberi* (L.), *Pleurophorus caesus* (Creutz.), *Copris lunaris* (L.), *and Euoniticellus fulvus* (Goeze)) are rare today and primarily associated with sandy and heavily disturbed ground. This strongly suggests that the lowland river valleys in at least this particular interglacial were heavily grazed and that herbivores had a pronounced formative effect on the landscape.

'Dung beetles' have featured in discussions concerning the nature and use of Holocene woodland as well. Many valley fen and riverside deposits from the Early and Middle Holocene contain 'dung beetles' that account for between 5 and 10% of the terrestrial faunas recovered (Whitehouse and Smith, 2010). The presence of these taxa has been used to support the proposition by Frans Vera (2000) that Holocene woodlands contained substantial areas of open grassland and clearings, which were created and maintained by large numbers of grazing herbivores (Svenning, 2002). This conclusion has been recently questioned (Mitchell, 2005; Whitehouse and Smith, 2010) but considerable confusion surrounds the issue of what a 5–10% contribution of 'dung beetles' as a proportion of terrestrial insect faunas actually represents in terms of herbivore herd size and concentration (Smith et al. 2010). A related issue is implied in archaeological discussions that have centred on the use of Neolithic woodland as areas for grazing by domestic animals. Girling (1989) and Robinson (2000) have argued, based on a 10–15% occurrence of 'dung beetles' in the terrestrial fauna at a number of archaeological sites, that herds of domestic animals were 'set loose' to browse in valley woodland. However, both the size of these herds and whether they were associated with domestic stock or wild animals such as deer remains unclear (Whitehouse and Smith, 2010).

Similarly, a number of insect faunas have now been recovered from a range of Late Bronze Age, Iron Age, and Roman field systems in the South East and Midlands of England (e.g. Robinson, 1979, 1993; Lewis et al. 2006; Smith, 2011). Farmoor and Minges Ditches in Oxfordshire (Robinson, 1979, 1993), several sites near Heathrow in Middlesex (Lewis et al. 2006), Little Paxton in Cambridgeshire (Smith, 2011), and Whitemoor Haye in Staffordshire (Smith, 2002) have produced insect assemblages that contain a wide range of Scarabaeidae dung beetles that are common today in farmed pastures (Jessop, 1986). These taxa, along with members of the wider 'dung beetle community', can account for between 20 and 40% of the terrestrial fauna. However, other field systems, or parts of field systems, from the same period have yielded a very limited range of 'dung beetles' that do not make a substantial contribution to the terrestrial fauna, for example, those from Mount Farm and Barton Court Farm in Oxfordshire (Robinson, 1983). This might imply, as suggested by Robinson (1983), that dung beetle communities could be used to test whether field systems were arable, mixed or mainly used for pasture.

2.2. Can the proportions of 'dung beetles' from palaeo- and archaeo-entomological samples indicate the density of grazing?

It has often been assumed that the relative proportions of taxonomic or ecological groups within sub-fossil insect faunas have no real meaning in terms of landscape interpretation (but see Robinson, 1983). At best, the statistics are difficult to interpret directly and, at worst, are thought to have no real meaning. Several pieces of analogue work in the past have clearly outlined the nature of the problem (e.g. Kenward, 1975, 1978, 1982; Smith, 1998). Terrestrial insects, such as 'dung beetles', appear to enter depositional environments (such as bodies of open water) by a number of complex taphonomic routes. This means that their numerical occurrence may not accurately reflect the past contribution that grazing or grassland may have made to an archaeological landscape (Kenward, 1975, 1978). This may be particularly true of the *Aphodius* 'dung beetles', that fly very readily and have a tendency to disperse widely across the landscape as they search for suitable breeding and feeding sites (Kenward, 1975, 1978; Jessop, 1986). One of the key results of Kenward's (1975) 'York drain' experiment was the realisation that potentially large numbers of 'dung beetles' could enter deposits that were a considerable distance away from the nearest area of grazing and pasture. This has led to an unfortunate tendency to think that any consideration of percentage occurrence of 'dung beetles' in archaeological and palaeoecological deposits as being essentially meaningless.

2.3. Can the types of 'dung beetles' recovered indicate the types of herbivores present?

There also seems to be an 'unwritten rule' within archaeoentomology and palaeoentomology that 'dung beetles' cannot be used directly to indicate which species of grazing animal(s) may have been present in the landscape. This is understandable; a quick scan of the literature on dung beetles (Scarabaeidae in particular) suggests that many species do not show a specific preference for the dung of a particular herbivore, but are opportunistic (i.e. the 'host preferences' in Jessop (1986) and Koch (1989) are often non-specific). It has been suggested that this is because dung beetles tend to exploit a resource that is patchy and short-lived (Robinson, 1983). The beetles therefore have to be generalist (polyphagous) in their approach and cannot be over-specific in their preferences. It is often thought, therefore, that the resource partitioning of 'dung beetles' is very broad and has considerable overlap (i.e. Gittings and Giller 1998; Hanski, 1991).

However, recent work has begun to suggest that there may be more general food preferences (trophic habitat separation) shown by the Scarabaeidae in terms of the types of herbivore dung chosen. This is the difference between 'specialist' taxa that might only be associated with a single herbivore and those that favour the dung of a range of browsers (leaf and shoot feeders) but are not interested in the dung of grazers (mainly grass feeders). In essence, these taxa may show a 'broad preference' for the dung of one type, or species

of herbivore over another, if they have a choice (Finn and Giller 2002). Recent field tests have shown that if cattle, sheep and deer are present in the same area, the dung of the three animals will often contain the same range of Scarabaeidae dung beetles, but that one or two particular species will be much more common in one type of dung than the others (Weβmer 1995; Barbero et al. 1999; Dormont et al. 2004, 2007; Gitting and Giller 1988; Finn and Giller, 2002). However, little specific research seems to have been done to see whether there is any broad separation between the dung of ruminants and non-ruminants and between grazers and browsers in terms of the range of associated 'dung beetles'.

Research on Pleistocene insect faunas may also help to clarify this issue. The 'dung beetles' associated with the remains of Pleistocene woolly mammoths (*Mammuthus primigenius* Blumenbach) found at Condover, Shropshire (Allen et al. 2009) and Lynford, Norfolk (Coope, 2012), with Steppe Mammoth (*Mammuthus trogontherii* Pohlig) at West Runton, Norfolk (Coope, 2000) and with the straight-tusked elephant (*Palaeoloxodon antiquus* Falconer and Cautley) at Aveley, Essex are quite different in their composition from those found in the Holocene. This provisionally suggests that 'dung beetle' populations may, in general, respond to distribution patterns of herbivores, the impact on vegetation and the changing nature of the landscapes herbivores produce.

It is also apparent that geographic factors, season, vegetation cover, local soil condition, humidity, the relative water content of the dung, and the size of the pat and time since defecation may also be determining factors for the range of dung beetles recovered (Koskela and Hanski, 1977; Gittings and Giller 1988; Hanski, 1991; Barbero et. al., 1999; Finn and Giller, 2002; Carpaneto et al. 2005). Weβmer (1994, 1995) suggests that the dominant factor is related to season, with other factors having less importance. The lack of understanding concerning the driving factors behind dung beetle occurrence is best articulated by Gittings and Giller (1988, 582), who note that "evidence from the literature on dung beetle preferences for different types of dung is scanty and somewhat contradictory"

3. Methods

Here we describe two analogue studies on modern dung beetle populations to with the aim of investigating the potential of these taxa to address the issues raised above. The use of analogue faunas to examine comparable issues is well established and validated within archaeoentomology and palaeoecology (e.g. Kenward, 1975, 1982, 2006; Robinson, 1983; Smith, 1996, 1998, 2000; Smith et al. 1999, 2010). A comparison between the analogue and the past is not about using the data (the insect fauna) as a direct mirror to the past but rather to demonstrate that it is possible to use insect faunas from the modern world to address the archaeological/palaeoecological issue being researched. Though the individual taxa may change between the past and the present, the general nature of the fauna, the effects that circumstances have on that fauna, and the approach taken remain valid (see Smith et al. 2010).

Two types of analogue studies are described here. The fieldwork at Dunham Massey, Cheshire and Epping Forest, London examined the insect faunas from a series of sediment samples taken from ponds in heavily grazed parkland at Dunham Massey; and ungrazed woodland at Epping Forest (Smith et al., 2010). Both studies aimed to examine the extent to which the proportion of 'dung beetles' in the terrestrial faunas reflected the concentration of local herds. The second set of studies described here, from the Wildwood Trust and Stodmarsh NNR in Kent, and Chillingham Park in Northumberland, aim to examine the extent to which the recovered 'dung beetles' varied between the dung of different species of large mammals. Differences in methodology at each of the study sites reflect different research goals of the overall projects at each site (see Smith et al. 2010); issues of inter-site comparability are discussed at length below. The locations of the sites used in this study are indicated in Fig. 1.

3.1. Fieldwork and investigations at Dunham Massey and Epping Forest

The Old Park at Dunham Massey, Cheshire, is a 101 ha deer park that is grazed by a herd of around 250 fallow deer (*Dama dama* (L.). Epping Forest (London Borough of Epping Forest District) is a 2430 ha area of dense deciduous woodland interspersed with open grassy 'plains' and home to a population of around 500 individuals of muntjac deer (*Muntiacus reevesi* (Ogilvy)) and fallow deer along with a small seasonal herd of cattle (*Bos taurus* L.). Recent sediments (probably representing less than ten years of accumulation) were sampled from the bottom of the ponds at both sites using a Ponar grab sampler. Five samples were taken from each of four ponds at Dunham Massey and five samples from four ponds at Epping Forest, representing a total of 40 samples in total. A volume of around ten litres of sediment was sampled from each of the individual sampling sites.

Insect remains were extracted from the material using the standard procedure of paraffin flotation outlined by Kenward et al. (1980). The aim was to recover the sub-fossil fauna in such a way that sampling and depositional history would match similar water-lain deposits in the archaeological and palaeoecological record. The coleopterous (beetle) faunas recovered were identified using a range of biological keys and by direct comparison to the Gorham and Girling collections housed at the University of Birmingham.

The insects recovered from the ponds at Dunham Massey and Epping Forest were assigned to a range of ecological groups based on the scheme outlined by Robinson (1981, 1983), which includes one that is exclusive to 'dung beetles' (group 'df' – in Smith et al. 2010). The ecological significance of the overall results from the sites is explored in Smith et al. (2010).

3.2. Field work and investigations at the Wildwood Trust, Stodmarsh and Chillingham

3.2.1. Wildwood Trust

The Wildwood Trust, Kent is a 40 ha zoological park that contains around 300 specimens of a range of species that were either present themselves in the Late Pleistocene and Early Holocene in Britain or represent close relatives of now-extinct forms. These include Konik horses (*Equus caballus* (L.)) (the result of an attempt to breed back to the European tarpan (*Equus ferus ferus* (Boddaert)) in the latter part of the 18th century), red deer (*Cervus elaphus* (L.)) and wild boar (*Sus scrofa* (L.)). These animals are allowed to roam in large wooded enclosures and are fed with a range of prepared and commercial feeds.

Sampling at Wildwood occurred late in July 2010. Four samples of dung were taken each from the Konik, red deer and wild boar enclosures. The material was usually around 3–4 L in volume. The dung was placed in a bucket of water and the larger organic component was kept under the surface using a 4 cm mesh sieve. The 'dung beetles' were collected as they floated to the surface of the water in the bucket. This process was continued, with periodic stirring of the material, until all live insects were extracted.

3.2.2. Stodmarsh

Stodmarsh is a 165 ha National Nature Reserve (NNR) located in the Stour Valley in north Kent. It contains a mix of grazing marsh, meadowlands, reed bed and open water crossed by a maze of

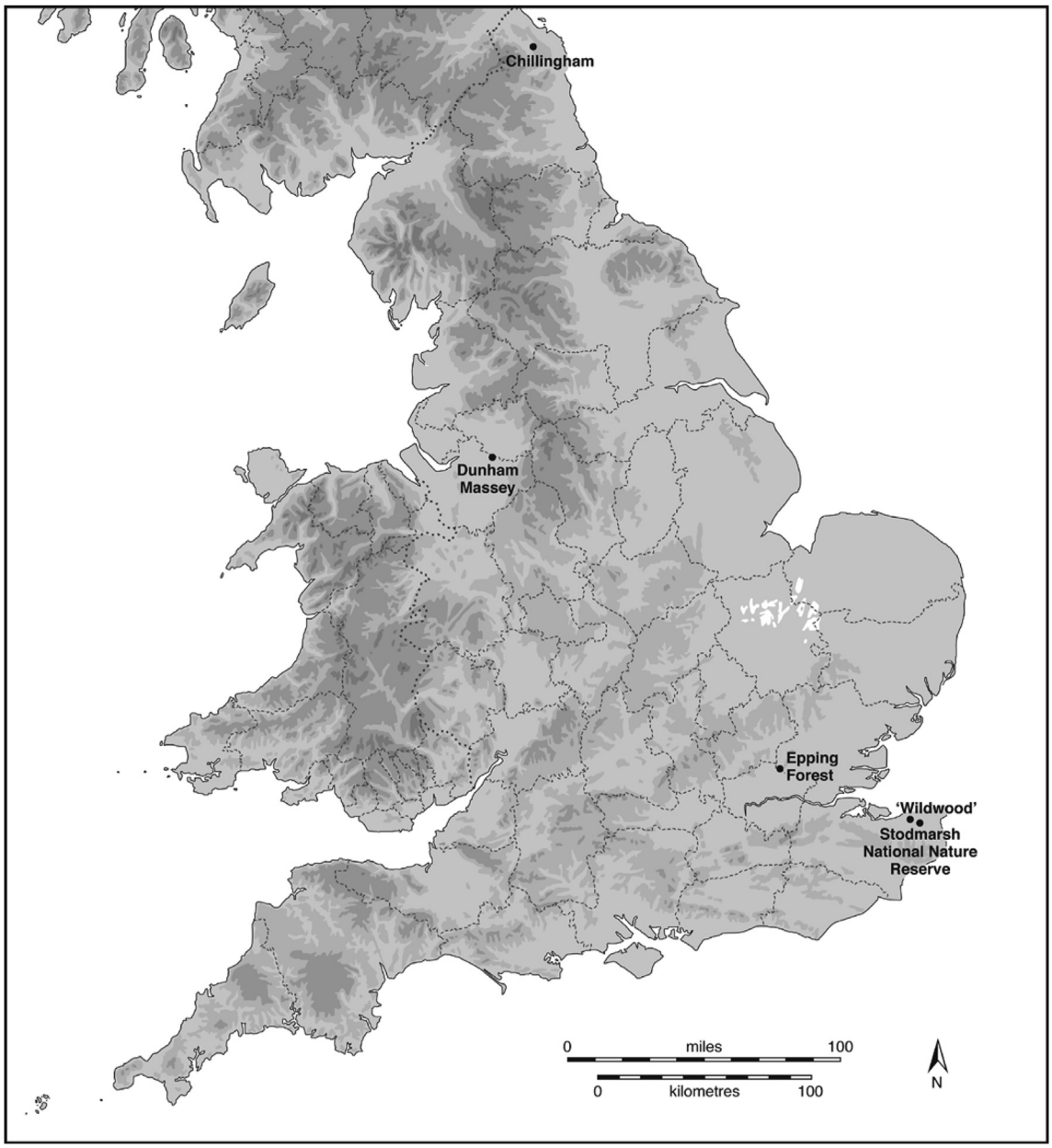

Fig. 1. Map of the sites discussed.

vegetationally diverse ditches. Today, the wet grassland is managed for conservation grazing purposes by a herd of 15–20 Konik horses owned by the Wildwood Trust. The welfare of the horses is monitored but no supplementary feeding occurs.

Five samples of dung were collected from the Konik herd in early July 2010 and were also around 4–5 L in volume. These were washed, dried and then sorted by hand to extract the dead insects prior to identification.

3.2.3. Chillingham

Chillingham Park, Northumberland, is home to the Chillingham 'Wild White Cattle'. These cattle are believed to be descendants of a herd of domestic cattle that was brought together in the late medieval period. They are distinct from modern cattle both in form and behaviour and are widely regarded as an archaic and 'unimproved' breed. Today, the herd is enclosed in a 130 ha 'pasture woodland' enclosure on the estate. Though their welfare is monitored, they are left to graze and organise their herd structure with minimal human interference. Samples of dung from the Chillingham herd were collected in late August 2011 and were around 1–2 L in volume.

Pictures of the 'donors' of the sampled material are shown in Fig. 2 and of the types of dung sampled in Fig. 3.

4. Results

4.1. Proportions of 'dung beetles' from Dunham Massey and Epping ponds

The beetle fauna recovered from the ponds at Dunham Massey and Epping Forest were presented in Table 3 in Smith et al. (2010). Fig. 4 presents the proportions of 'dung beetles' as a percentage of

Fig. 2. Animals that provided dung samples (a) cattle at Chillingham, (b) Konik at Stodmarsh, (c) Red deer at Wildwood, (d) wild boar at Wildwood).

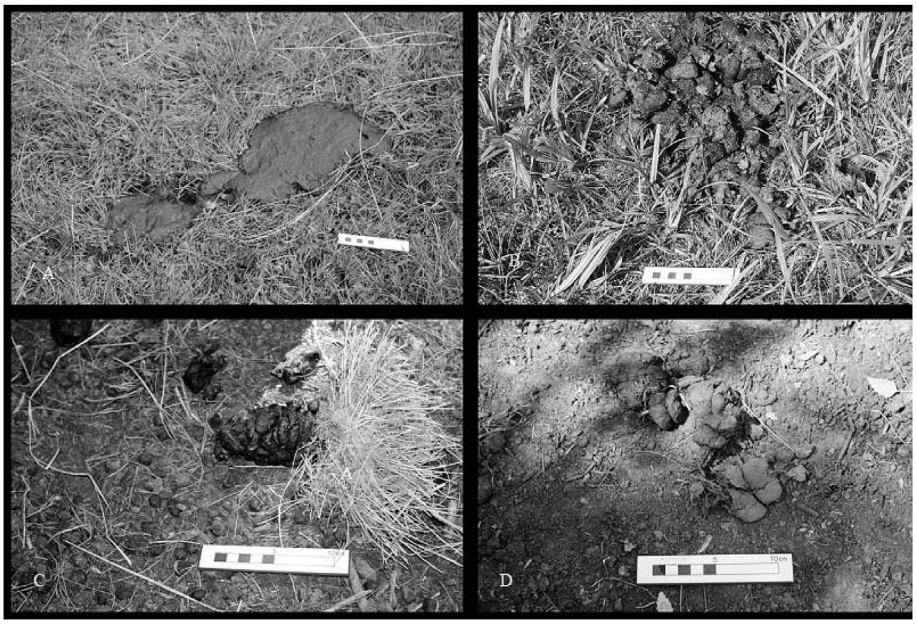

Fig. 3. Examples of animal dung (a) cattle dung, (b) Konik dung, (c) red deer dung, (d) wild boar dung (scale = 10 cm)).

the terrestrial fauna recovered from these pond samples. The 'dung beetles' recovered at both sites are from a relatively limited range of species. These are mostly a number of hydrophilids such as *Cercyon impressus, Cercyon haemorrhoidalis, C. atricapillus* and *C. analis*. In terms of Scarabaeidae, the ponds at Dunham Massey produced comparatively more individuals than those at Epping, mainly the 'generalist' *Aphodius sphacelatus*. Between 3 and 16 individuals of dung beetles were recovered from the individual ponds at Dunham Massey. At Epping, the Scarabaeidae fauna is much smaller in number (between 1 and 5 individuals per pond) but contained one individual of *Aphodius zenkeri* (from Alder pond), which is almost exclusively associated with dung in woodland (and here, in deer dung) (Jessop, 1986; Koch, 1989; Weβmer 1995). Generally, the 'dung beetles' account for a higher proportion of the terrestrial fauna at Dunham Massey (15.8% at Island Pond, 7.6% at Old Man's Pond and 10.6% at Smithy Pond) than at Epping (4.2% at Alder Pond, 0.6% at Baldwin's Pond, 2.8% at Fairmead Pond and 1.9% at Lost Pond).

4.2. Dung pat beetles from Wildwood, Stodmarsh and Chillingham

The beetle fauna recovered from the sampled dung at Wildwood, Stodmarsh and Chillingham is summarised in Tables 1and 2 and Fig. 5. The nomenclature and taxonomic order follows Lucht (1987). The numbers in the table represent the number of individuals (MNI) recovered. Fig. 5 displays the number of individuals and the number of taxa recovered from the dung pats. Table 2 is a summary of the occurrence of the main families of 'dung beetles'

Table 1
The coleopterous fauna recovered from the animal dung (nomenclature follows that of Lucht 1979).

Site	Ecological codes	Wildwood												Chilingham						Stodmarsh				
Herbivore		Konik				Boar				Deer				Cattle						Konik				
Sample		1	2	3	4	Pru 2	Pru 1	Boris 1	Boris 2	1	2	3	4	1	2	3	4	5	6	1	2	3	4	5
Hydraenidae																								
Helophorus spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Hydrophilidae																								
Sphaeridium scarabaeoides (L.)	rf	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	6	6	–	–	11	–	2	8
Sphaeridium lunatum F.	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Cercyon impressus (Sturm)	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	36	–	–	18	1	–	–
Cercyon haemorrhoidalis (F.)	rf	–	4	6	4	–	–	–	3	1	–	–	–	–	–	–	–	–	1	–	10	1	89	45
Cercyon melanocephalus (L.)	rf	4	1	20	4	–	–	–	–	–	–	–	–	19	13	–	2	4	–	–	19	–	2	7
Cercyon quisquilius (L.)	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	79	–	13	14
Cercyon pygmaeus (Ill.)	rf	–	6	3	2	–	–	1	–	–	–	–	–	–	–	–	14	3	–	8	200	–	35	81
Cryptopleurum minutum (F.)	rf	22	11	6	3	1	–	1	1	–	–	–	–	–	–	–	–	–	1	1	–	–	1	6
Clamdidae																								
Clambus punctulum (Beck)		–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ptiliidae																								
Ptillidae Gen. & spp. indet.	rt	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	18	10	3	–	1
Ptenidium pusillium (Gyll.)	rt	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acrotrichis sericans(Heer)	rt	–	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acrotrichis spp.	rt	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Staphylinidae																								
Megarthrus depressus (Payk.)		2	1	1	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	1	–	–
Omalium italicum Bernh.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Oxytelus laqueatus (Marsh.)	rf	5	2	2	3	–	–	–	3	–	–	–	–	10	10	–	18	7	6	1	1	–	–	1
Oxytelus sculpturatus Grav.	rt	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxytelus nitidulus Grav.	rt-d	4	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	5		10	8
Oxytelus complanatus Er.	rt	–	–	–	–	–	–	5	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Oxytelus tetracarinatus (Block)	rt	50	14	13	5	–	–	7	1	–	–	–	–	–	1	–	12	–	15	30	5	6	4	8
Platystethus arenarius (Fourc.)	rf	1	–	–	1	–	–	5	–	–	–	–	–	–	1	–	7	3	–	–	–	–	–	1
Stilicus orbiculatus (Payk.)		–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Xantholinus linearis (OL.)	rt	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Philonthus cruentatus (Gm.)		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Philonthus splendens (F.)	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Philonthus fimetarius (Grav.)	rf	1	–	1	2	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Philonthus marginatus (Müll.)	df	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–
Philonthus spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Tachinus rufipes (Geer.)	u	11	–	6	9	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucoparyphus silphoides (L.)	rt	6	1	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Autalia rivularis (Grav.)		3	1	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aleochara lanuginosa Grav.		2	–	–	–	3	1	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Aleochara bipustulata (L.)		–	–	–	–	10	5	11	3	–	1	–	–	–	–	–	–	–	–	3	–	–	1	–
Aleocharaspp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	1	–	–
Aleocharinidae Genus & spp. Indet.		16	31	27	16	2	2	4	9	–	–	–	–	–	–	–	–	–	1	1	3	–	–	–
Cucujidae																								
Monotoma brevicollis Aubé		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Cryptophagidae																								
Telmatophilus typhae (Fall.)		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Endomychidae																								
Mycetaea hirta (Marsh.)	rd-h	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Scarabaeidae																								
Onthophagus similis (Scriba)	oa-rf	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aphodius erraticus (L.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	2	2
Aphodius haemorrhoidalis (L.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1
Aphodius rufipes (L.)	oa-rf	–	–	–	–	3	–	–	–	–	–	–	–	3	–	4	–	2	–	1	–	–	–	–
Aphodius zenkeri Germ.	oa-rf	–	–	–	–	–	–	9	6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aphodius equestris (Panz.)	oa-rf	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aphodius contaminatus (Hbst.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Aphodius sphacelatus (Panz.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
*Aphodius prodromus (*Brahm)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	–	–	–	–	–	–	–
Aphodius fimetarius (L.)	oa-rf	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
Aphodius rufus Moll.	oa-rf	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Curculionidae																								
Barypeithes sulcifrons (Bohe)	oa	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total number of individuals		131	76	95	57	26	10	47	28	4	2	0	0	37	33	0	70	63	26	68	366	17	162	186
Number of taxa		15	12	16	15	10	5	12	9	4	2	0	0	7	7	0	11	8	7	11	14	10	11	16

Ecological coding follows that of Kenward and Hall 1995. oa = usually not associated with settlement. rf = rotting foul often animal dung. rt = rotting plant material. rd-h = associated with drier organic material in settlement.

Table 2
Summary of the occurrence of the main families of the beetle faunas recovered from Wildwood, Stodmarsh and Chillingham. Underlined species seem particularly significant.

'Donor' species	Site	Hydrophilidae	Staphylinidae	Scarabaeidae
Horse	Wildwood	*Cercyon haemorrhoidalis* *C. melanocephalus* *C. pygmaeus*	*Oxytelus tetracarinatus* *O. laqueatus* *Tachinus rufipes* *Autalia rivularis* *A. langinosa*	X
	Stodmarsh	*Sphaeridium scarabaeoides* *Cercyon impressus* *C. haemorrhoidalis* *C. quisquilius* *C. melanocephalus* *C. pygmaeus*	*Oxytelus nitidulus* *O. tetracarinatus* *Aleochara bipustulata*	*Aphodius erraticus* *A. haemorrhoidalis*
Cattle	Chillingham	*Sphaeridium scarabaeoides* *Cercyon impressus* *C. melanocephalus* *C. pygmaeus*	*Oxytelus tetracarinatus* *O. laqueatus* *Platystethus arenarius* *Philonthus marginatus* *P. splendens*	*Aphodius rufipes* *A. prodromus*
Red Deer	Wildwood	X	X	X
Boar	Wildwood	X	*Oxytelus complanatus* *O. tetracarinatus* *Aleochara lanuginosa* *A. bipustulata*	*Aphodius zenkeri* *A. equestris*

recovered from the four main types of animal dung. Species that are underlined appear to represent a dominant aspect of the faunas.

4.2.1. Chillingham: cattle dung

Fig. 5 suggests that cattle dung produced relatively lower numbers of individuals compared with horse dung. However, the cow pats at Chillingham were very flat and thin compared to the more substantial 'piles' of horse dung sampled at Wildwood and Stodmarsh (Fig. 3). As a result, at Chillingham it was only possible to collect samples of dung that were around a quarter of the volume compared to those collected from the other species. If similar volumes of cattle dung had been collected, the numerical size of the beetle fauna would probably have been comparable to the dung of Konik horses at Wildwood and Stodmarsh.

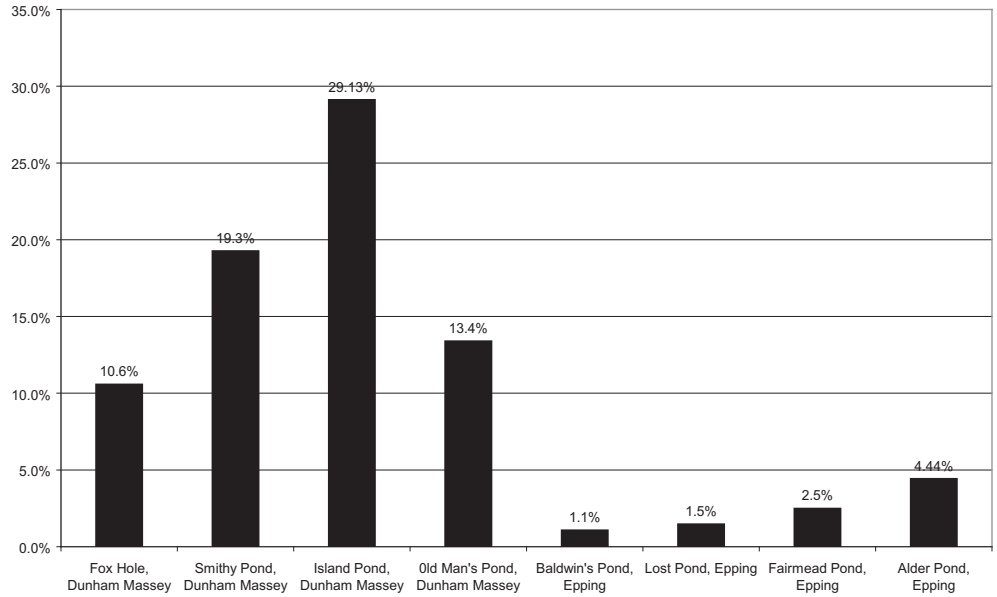

Fig. 4. The relative proportions of taxa associated with dung (df) from Dunham Massey and Epping (see Smith et al. 2010 for full data).

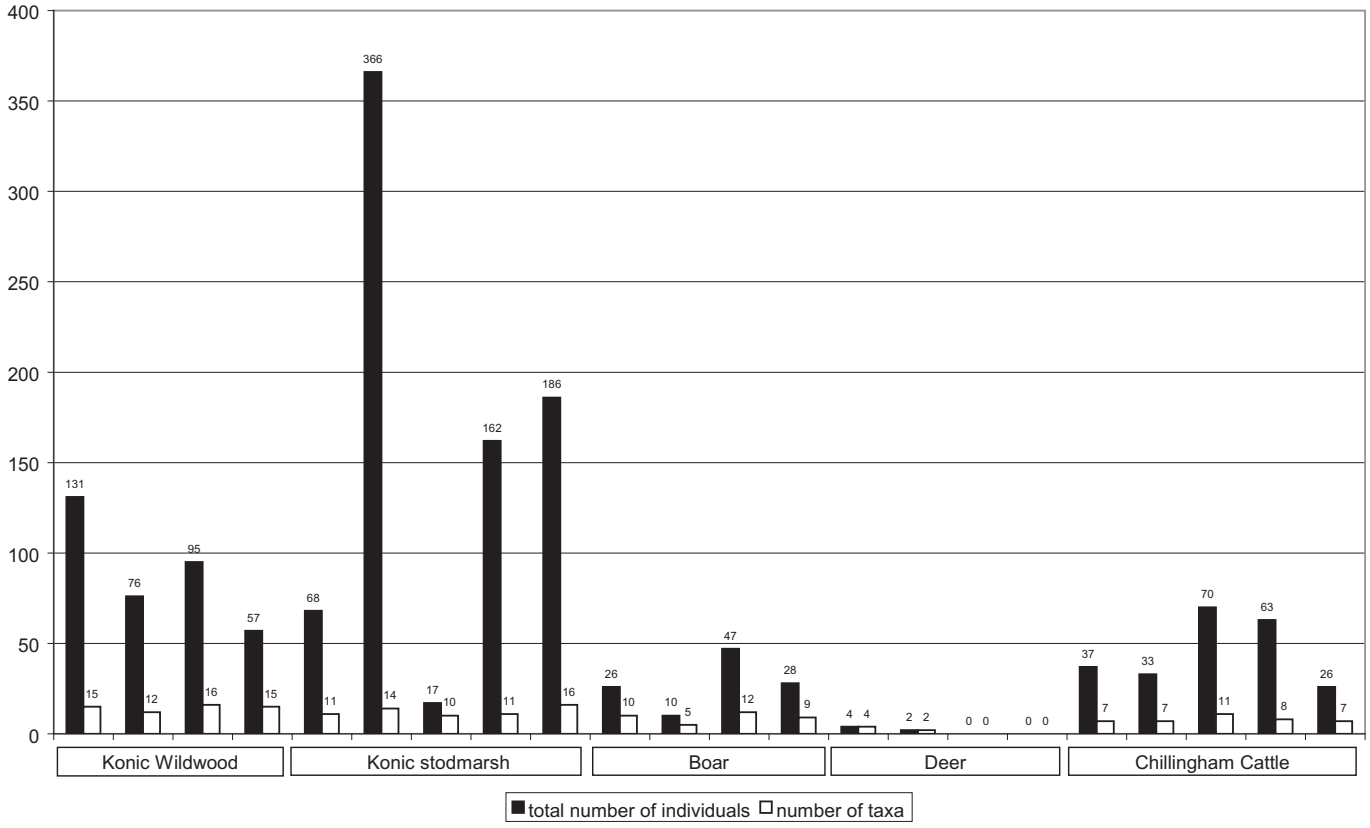

Fig. 5. Number of individuals and number of taxa from the dung pats.

The beetles recovered from the cattle dung from Chillingham could be considered an example of a 'classic dung beetle fauna'. *Sphaeridium scarabaeoides* is usually exclusive to animal dung, often that of cattle (Hansen, 1987). However, it can be found in a range of very fluid and wet organic matter such as stabling material (Hansen, 1987; Koch, 1989). The three species of *Cercyon* recovered (*Cercyon impressus, Cercyon melanocephalus and Cercyon pygmaeus*) are often associated with animal dung, but also can occur in a much wider range of wet and decaying plant materials (Hansen, 1987; Koch, 1989). *Oxytelus laqueatus* and *Platystethus arenarius* are almost exclusive to animal dung, often occurring in very large numbers (Tottenham 1954; Lott, 2009). *Philonthus marginatus* and *Philonthus splendens* are common in, though not exclusive to, animal dung that has become quite dry (Koch, 1989). The two Scarabaeidae dung beetles recovered from the cattle dung, *Aphodius rufipes* and *Aphodius prodromus*, are considered to be very generalist in their preferences and are quite common in modern animal dung (Jessop, 1986). Drawing upon archaeological data, Carrott and Kenward (2001) and Kenward et al. (2004) have suggested that both of these *Aphodius* species were likely able to breed in the wetter and fouler parts of human habitation.

4.2.2. Wildwood and Stodmarsh: Konik dung

The Konik horse dung, sampled from both Wildwood and Stodmarsh, produced a large number of individuals per dung pat but these 'dung beetles' are derived from a comparatively restricted range of insects. This range of species, to some extent, departs from the 'classic community' seen in the Chillingham cattle dung. Again, relatively large numbers of *Cercyon* beetles were recovered, with *Cercyon quisquilius* occurring in very large numbers at Stodmarsh. *C. quisquilius* is common in animal dung but Hansen (1987) and Koch (1989) suggest that it is also abundant in wet decaying vegetation. Except for *Oxytelus laqueatus*, the staphylinids recovered are quite different in their nature to those seen in the cattle dung. *Oxytelus tetracarinatus, Oxytelus nitidulus, Tachinus rufipes, Autalia rivularis* and *Aleochara lanuginosa* are all species that are common in loose structured and decaying plant materials, such as compost heaps and stabling waste, as well as in animal dung (Tottenham 1954; Koch, 1989; Lott, 2009). Many of these taxa are also commonly found in archaeological contexts where they are again associated with loose structured waste materials and stabling matter (Kenward and Hall, 1995, 1997; Smith, 2000; Carrott and Kenward, 2001). Welch (1997) suggests that *Aleochara bipustulata* (recovered from Stodmarsh) is usually associated with sheep, horse and dog dung. No Scarabaeidae dung beetles were recovered from the Konik dung at Wildwood. Two *Aphodius* dung beetles were found in small numbers from the Konik dung at Stodmarsh. *Aphodius erraticus* and *Aphodius haemorrhoidalis* are often associated with horse, sheep and to a lesser extent cattle dung in open areas (Jessop 1987).

4.2.3. Wildwood: red deer dung

The four samples of deer dung from Wildwood produced a very small fauna of insects with only one taxa, *Aphodius rufus*, specifically associated with animal dung.

4.2.4. Wildwood: wild boar dung

Wild boar dung also produced comparatively low number of individuals compared to the horse and cattle dung. No hydrophilids were recovered. The staphylinids were dominated by *Aleochara bipustulata,* which tends to be associated with the drier dung of dog, sheep and horse (Welch, 1997). *Aphodius zenkeri* was recovered in relatively large numbers from the wild boar dung and is

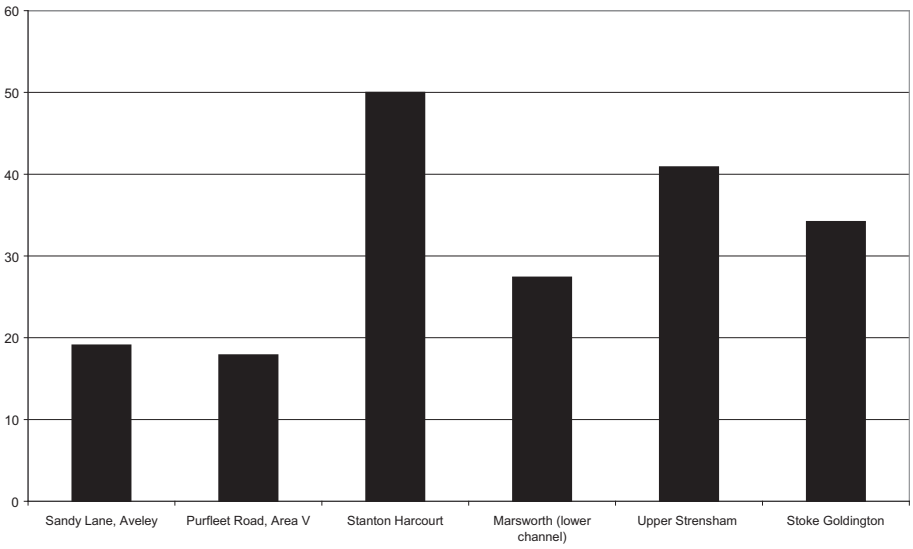

Fig. 6. Proportions of dung beetles from a range of terrestrial insect faunas from a range of MIS 7 sites.

frequently associated with dung, often deer, in woodland (Weßmer 1995), as is *Aphodius equestris* (Jessop, 1986).

5. Discussion

5.1. Can the proportions of 'dung beetles' in palaeo- and archaeo-entomological faunas indicate herd concentration?

The modern analogue work from the ponds at Dunham Massey and Epping suggests that the proportions of 'dung beetles' in terrestrial faunas can separate landscapes where the level of grazing is relatively low from those where it is relatively high and where animals are heavily concentrated. If the data presented here are taken at face value, it might be suggested that where 'dung beetles' (of all types) account for <10% of the palaeoecological terrestrial fauna, we are most likely dealing with low densities of animals spread widely across the landscape. Conversely, values of >20% are suggested to indicate high densities of grazing animals, or at least local herd concentrations (Smith et al. 2010). These data appear to support the conclusions reached by Robinson (1983) who used the results of a number of pit fall and sweeping surveys to suggest that there was an intrinsic difference in the insect faunas from pasture on one hand and arable fields on the other.

If this 'rule of thumb' is accepted, this leads to a number of interesting conclusions about past insect faunas and what they might indicate about herd densities and strategies. Though the proportions of 'dung beetles' in Pleistocene deposits have not been routinely calculated, a simple scan of the available species lists (all contained in Buckland and Buckland, 2006) suggests that they are often a dominant part of these faunas. This can be seen in some recent work on the insect fauna from the Sandy Lane and Purfleet Road sites at Aveley, Essex (Schreve et al., unpublished data) which date to the penultimate interglacial (MIS 7 c. 240–200 ka) (Schreve, 2004). Dung beetles were relatively common in the terrestrial faunas at both sites with values close to 20% (see Fig. 6) (Schreve et al., unpublished data). These proportions are similar to those recovered from the modern ponds at Dunham Massey, suggesting that large herbivores must have been as dominant a part of the Pleistocene landscape as they are in this modern deer park. A comparison with other MIS 7 sites (Whitehouse et al. 2013; unpublished data) (Fig. 6) indicates that in a range of deposits, often associated with the remains of large herbivores, dung beetles can account for up to 50% of the insect faunas recovered. At a minimum, this at least implies sizeable herds of large grazing animals present and highlights the important role that large herbivores must have played in shaping these interglacial environments.

Similar arguments could also be made for the issue of Holocene woodland grazing by domestic livestock. In the majority of the Holocene sites examined by Whitehouse and Smith (2010), 'dung beetle' values are routinely below 20% of the terrestrial fauna. This perhaps indicates that 'Neolithic grazing' of domestic livestock was limited in extent or, if the 'dung beetles' were associated with the dung of wild animals, these were present in concentrations more similar to those at Epping rather than in the deer park at Dunham Massey. If this proposition holds true, it may be possible to use the proportions of 'dung beetles' in the terrestrial fauna to identify which archaeological landscapes and field systems from later prehistory were associated with domestic livestock and those that were intensively grazed. For example, the late 2nd to 4th century AD riverside 'ladder' field system at Little Paxton, Cambridgeshire, produced six insect faunas for which 'dung beetles' accounted for between 22 and 25% of terrestrial taxa recovered (Smith, 2011). This clearly suggests that this field system was pastoral rather than arable. A similar approach was also taken by Robinson in his comparative survey of a number of Iron Age insect faunas from the Thames Valley (Robinson, 1983).

Despite the evident potential of the approach taken here, conclusions must be drawn with care and a number of recommendations for future research can be made. The data concerning relative proportions of dung beetles as part of terrestrial faunas are only derived from a limited number of samples from two modern study locations (Dunham Massey and Epping). Furthermore, one of these (Dunham Massey) is a deer park where the concentration of animals may be unnaturally high. A wider range of sites, with different concentrations of animals, thus needs to be investigated before firmer conclusions can be drawn. At present these data are also solely based on a study of one large animal – fallow deer. The same type of experiment should consequently be repeated with a wider range of animals including domestic livestock as well as 'wild' animals.

Taphonomic considerations and how the archaeological and palaeoecological records form should also be taken into account. In

this study the samples were deliberately taken from small, still-water ponds. The majority of Pleistocene and Holocene sites, however, are associated with river systems, alder carrs, raised bogs and, in the case of Late Holocene archaeological sites, ditches in field systems where depositional patterns are less clear and largely unstudied.

Several issues concerning sampling also need to be investigated further. 'Dor beetles' (*Geotrupes* spp.) were absent from these faunas. One of the reviewers of this paper and Weßmer (1995) suggest that *Geotrupes, Onthophagus*, and other tunnellers, rapidly retreat into their burrows when the dung is disturbed leaving only a few seconds to collect them. This suggests that the strategies used to collect the 'whole' fauna from the dung affects species representation needs to evaluated.

5.2. Can we use dung beetles assemblages to identify specific animals in the landscape?

The results presented here suggest that it is possible to distinguish four separate large mammal species on the basis of beetle assemblages associated with their dung. It is also clear that cattle and horse dung produce much larger populations of 'dung beetles' than either deer or wild boar. Furthermore, there appear to be intrinsic differences in the major groupings of beetles recovered, particularly where the staphylinids and scarabaeids are concerned. This raises the possibility that grazers (grass and herb feeders such as horse and cattle) can be separated from browsers (deer) and that both of these can be differentiated from omnivores (wild boars). Boar dung in particular has been reported to be is particularly unattractive to Scarabaeidae (Barbero et al. 1999).

The results of the present study may reveal why this occurs. Both the Chillingham cattle and the Konik horses in this survey produced very large, wet and loosely-structured pats. In contrast the deer and wild boar dung samples although fresh, were dry to the point of near desiccation, very compacted and each 'pat' or 'pellet' very small in volume (Fig. 3). This is seemingly not related to a straightforward difference between monogastrics (e.g. horse, wild boar) and ruminants (cattle, deer) but reflects the overall efficiency of each taxon in extracting nutrients and water from their food source. Dryness of dung has been shown by experiments in Africa to be a limiting factor in terms of the number of Scarabaeidae dung beetles recovered (Gittings and Giller, 1998). This is specifically related to 'pellet size', suggesting that larger faecal masses desiccate at a slower rate. Dryness was cited as a factor in determining dung beetle populations in dog excrement in Rome (Carpaneto et al. 2005). One key aspect of this phenomenon is that both dry and very fluid materials prevent the oviposition of eggs by Scarabaeidae (Gittings and Giller, 1998). Gittings and Giller (1998) have also suggested that the volume and fragment size of fibre in the pats may also influence what can live and breed in dung. This may partially explain the difference in the community of beetles recovered between the Chillingham cattle and the Konik horses seen here. In Fig. 3, it is apparent that the plant materials in the Konik dung is very bulky, fibrous and less processed, as is typical for a monogastric animal and in contrast with cattle where plant remains are finely milled in a process characteristic of rumination. Similar conclusions were also reached by Weßmer (1995) who identified distinct differences in the fauna of 'dung beetles' recovered from sheep pellets and cow pats.

As with the studies reported above, conclusions must be drawn with care on the basis of a relatively modest data set but again a number of recommendations for future study can be made. For example, recordings of relative size, weight, volume, moisture and relative fibre content of dung pats could be taken. In addition, it should be borne in mind that none of the sampling sites represent completely 'wild' conditions. Although the animals were kept in large enclosures, they were not free to roam and, at the Wildwood Trust, part of the Koniks' diet comes from prepared animal feed as well as graze. This study also takes no account of factors such as variation in seasonality or the interval since defecation. These have all previously been identified as important factors in shaping the dung beetle community (Koskela and Hanski, 1977; Hanski, 1991; Weβmer, 1994, 1995; Gittings and Giller, 1998). Lastly, a much larger number of dung pats taken from a wider range of landscapes should be examined in future. Particularly important in terms of these analogues, especially those from the woodland in Epping and the Wildwood Trust, are the observations of Koskela and Hanski (1977) and Weßmer (1995) that suggest cow dung in woodland contained both a smaller population and diversity of 'dung beetles' than those from grassland.

Lastly, the modern insect faunas were recovered directly from dung pats. In contrast, most archaeoentomological and palaeoecological faunas come from former water bodies into which terrestrial insects have been washed in, been accidentally incorporated or occur as part of 'flight faunas' (*sensu* Kenward, 1978). We only are aware of one example from the archaeological record where the insects and plants sampled appear to have come *directly* from a dung pat. This is a closely-sampled deposit from the outer ditch at Banbury Castle dating to 1640–1778 AD (Smith and Smith, 2009 unpublished data). A sub-sample taken for plant macrofossils contained a superabundance of seeds from *Campanula* cf. *latifolia*(giant bell flower). The same sub-sample also contained large numbers of puparia of flies in the families Limosinidae and Sepsidae. These are typically associated with animal dung and human excrement (Smith, 1989). This combination of biological remains was interpreted as representing a single cow pat, which contained the remnants of a giant bell flower that had fallen directly into the ditch (Smith and Smith, 2009 unpublished report).

Though a larger study, similar to the case study described above, that examines beetles from dung pats might reinforce an association between specific herbivores and 'dung beetles', an additional component to this study would be needed in order to apply these results directly to the archaeological and palaeoecological record. 'Ponar sampling' of a series of nearby ponds or ditches in the same area as any 'dung pat' could be undertaken to produce data that are directly comparable to the archaeological and palaeoecological record.

6. Conclusions

The initial investigations of various herbivore dung pats described above have demonstrated the potential of 'dung beetles' as a proxy for answering questions about past herbivore presence, numbers and grazing intensity. This can be applied to a range of Pleistocene and Holocene deposits, even where no animal bones have been found.

However, the studies described above have, in the way most modern analogue studies tend to do, raised a number of additional questions and concerns that require further exploration. The ability of the proportions of dung beetles in terrestrial insect faunas to act as a direct indicator of herd concentration and density needs further analogue testing. A more comprehensive study would need to examine more samples taken from a wider range of environments with differing levels of herd density and composition than that undertaken here. Further research would need to consider variations in season, pat composition and so forth, in addition to the type(s) of animal concerned. Any further study would need to examine the dung of herds that are freer roaming than some of the animals examined here. Finally, as indicated above, the analogue study also should include samples taken from small water bodies

near grazing herds of varying size in order to make the results directly comparable to the palaeoenvironmental and archaeological records.

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